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THE SEXUAL CYCLES OF FISH IN A STUDY OF THE STRUCTURE OF A SPECIES AND THE FUNCTIONAL STRUCTURE OF THE RANGE

Ye.I. Alekseeva and F.Ye. Alekseev

The divisibility of a species into populations is the result of /28 limitations in reproductive contacts, right down to complete cessation, between local (or seasonal) intraspecies groupings. Reproductive independence is the the main criterion of a population, which represents an elementary self-reproducing grouping. Reproductive isolation in the simplest and most obvious case is the /29 consequence of the complete spatial isolation of a population. Such a situation is quite rare with respect to the major commercial species. Usually, such species have uninterrupted ranges, and the ranges of the populations forming them are in close contact, or overlap continuously or intermittently to varying degrees. Each population is ecologically specific [22]. The specific nature of populations is the result of adaptation to specific local conditions, particularly to the nature of seasonal cyclical changes in physical and biotic environmental factors.

In the ocean, a seasonal cycle of conditions is observed everywhere,

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independent of the latitude or depth, with the nature and amplitude of the cycle of conditions, of course, differing. Cyclical seasonal changes in the environment bring about corresponding seasonal cyclicity in the manifestation of all living function of organisms: feeding, growth, maturation, and spawning; whereas, local characteristics in the nature and amplitude of seasonal phenomena bring about corresponding interpopulation differences in the seasonal biological cycles.

Of all the inter-population differences of this kind, differences in reproductive cycles basically have a special role because they can sharply limit and even stop the flow of genes between neighbouring local groupings. Such isolation, partial or even complete, can emerge very rapidly only on the basis of differences in seasonal phenomena in adjacent biotopes without preliminary ecological and genetic differentiation of neighbouring groupings. On the other hand, with the presence of a substantial reduction in reproductive contacts, initiated as a result of the divergence in reproductive cycles, the genetic differentiation of populations can occur fairly rapidly. The divergence in reproductive cycles, governed by local differences in seasonal phenomena, can thus be regarded as the most important and widespread variant of the mechanism of "pre-copulation isolation" of E. Mayr [17]. Correspondingly, differences in the reproductive cycles of the groupings under investigation can be regarded as an important indication of their reproductive isolation, whereas the level of differences in the cycles can be regarded as an indicator of the degree of such isolation.

The level of divergence in the reproductive cycles generally corresponds to the level of differences in the course of seasonal phenomena within a species' range and is manifested particularly clearly in species with extensive zonal ranges in which the reproductive cycles of marginal groups can be oriented towards spawning in opposite seasons. Examples of this kind are fairly numerous. Thus, the common scad in the northern periphery of its range spawns in the spring and

summer at maximum temperatures [25]; and off the northwest coast of Africa - /30
in the autumn with the drop in temperature and in the winter up to early spring at minimum temperatures [20]. The Peruvian scad in subtropical and tropical latitudes in the region of the Naska Ridge spawns in the cold period, in August and September, and in notalian waters in the region of the Chilean trough - at the end of spring and in the summer of the Southern hemisphere, from November to February (our data). Sprats in the North Sea spawn in the spring and summer, and in the Black Sea - in the winter [14]. Mackerel, round sardinella and a number of other species with zonal ranges provide a similar picture [9, 1, 15, 27] in accordance with the familiar "Orton rules" [26]. The shift in reproductive cycles and their specific local nature in these examples are probably not directly determined by the thermal conditions, although they correlate well with them. The connection with temperature is formed through the course of the production cycles [19], whose distinguishing local characteristics are the main factor determining the orientation of the reproductive cycles of fish. When the differences in temperature conditions between the years is considerable, the spawning of temperate marine fish begins at fixed times, whereas in the tropics the begining deviates significantly from the average [16].

We used the parameters of the sexual cycles as a criterion for assessing the degree of divergence in the reproductive cycles. The sexual cycle is taken to mean the changes in the state of the gonads of sexually mature individuals in the period from the end of the previous spawning to the end of the next spawning. The sexual cycles were reconstructed on the basis of preliminary research on the distinctive features of the formation of expendable supply of oocytes, the nature of vitellogenesis and the type of spawning. At the same time, special attention was also given to relatively unstudied questions - of fundamental importance to the reconstruction of cycles - pertaining to the assessment of the approximate number

of batches and intervals between successive spawnings [3, 8, 7] in species with different types of batch spawning [6]. Thus, the description of the sexual cycles of the local groupings being studied was based on a preliminary study of the sexual cycles of individuals, particularly the duration of individual spawning periods.

In this study, some results are given of the study of individual aspects of the reproductive physiology of bigeye tuna (Thunnus obesus Lowe) and striped tuna (Katsuwonus pelamis Linne) of the Eastern-Tropical Atlantic, rock grenadier (Coryphaenoides rupestris Gunnerus) of the North-Atlantic ridge, South-Atlantic grenadier (C. holotrachys Gunther) of the Falkland-Patagonian region (42-52° S. lat.), red snapper (Beryx splendens Lowe) of the Atlantic Ocean and black scabbard (Aphanopus carbo Lowe) of the North Atlantic. The material was collected in 1970-1982.

The data on the visual determinations of the state of the gonads were /31
analyzed for more than 100 thousand specimens of the above-mentioned species of fish. The ovaries of 600 individuals were analyzed histologically. The size distributions of yellow oocytes were determined in the ovaries of 110 females.

Bigeye tune. The expendable supply of oocytes is formed according to K. Götting's continuous type, and vitellogenesis approximates the continuous-asynchronous type; spawning occurs in many batches with short intervals between batches. It was assumed earlier that spawning occurs year-round in the Tropical Atlantic [21, 23 et al.], that there are no fixed spawning grounds, and that the species is represented by a single population [10, 11].

On the basis of the analysis of the spatial and seasonal distribution of individuals with gonads in different phases of the sexual cycle, we established [7] that in the equatorial waters, between 10° N. lat. and 10° S. lat., there are two regions of massive spawning of bigeye tuna, localized west of the

centres of the northern and southern tropical cyclonic circulation. The reproductive cycles of tuna of the Northern and Southern hemispheres are oriented for spawning in the warm period, with maximums in June - September in the Northern hemisphere and in December - March in the Southern hemisphere. The Eastern-Tropical Atlantic is inhabited by two independent groupings (populations) of bigeye tuna with opposite-phased sexual cycles [7]. This conclusion is based on long-term data and is corroborated by the material collected in 1980. A typical picture of terminal spawning is observed in the southern region from February to April. The percentage of females with mature ovaries dropped from 70 to 14%, and spent females increased from 7 to 37%; and in April already approximately 20% of the females passed into stage III of maturity of the next sexual cycle. In the northern region in May, the state of the ovaries was characteristic of initial spawning: approximately 60% of the females were in stages IV and IV - V of maturity, the remainder were in the advanced stage III (Fig. 1).

Striped tuna. In contrast to bigeye tuna, the spawning of striped tuna in the Eastern-Tropical Atlantic is observed far beyond the limits of equatorial waters, right up to the 20th parallel of both hemispheres. At the same time, within equatorial waters, it occurs for most of the year, but its occurrence is reduced to two months towards the northern and southern peripheries.

Vitellogenis is interrupted-asynchronous, spawning occurs in batches with large intervals, and the number of batches is limited (3-4 batches). The tuna from equatorial waters do not differ from those caught in the northern and southern peripheries of the range in terms of the nature of spawning. The duration of individual spawning in this species is approximately 2-3 months, i.e. greater than the duration of group spawning noted in Senegal-Mauritania.

On the basis of an analysis of the distribution in space and time of /32 individuals in different phases of the sexual cycle, it was established that in

striped tuna the sexual cycles of the groupings of the Northern and Southern hemispheres are opposite-phased and oriented for spawning in the spring and summer of the corresponding hemisphere (Fig. 2). Both groupings begin to spwan in equatorial waters, but finish during the course of migration with spawning in northern and southern directions. The sharp reduction in the spawning period in the tropical peripheries of the reproductive region of the species' range, which does not conform with the considerable duration of individual spawning periods, is explained by the fact that individuals that are already finishing spawning, which was begun in the equatorial zone, reach the northern and southern limits of the reproductive region. Striped tuna is thus represented in the East Atlantic by two independent groupings - in the Northern and Southern hemispheres [24].

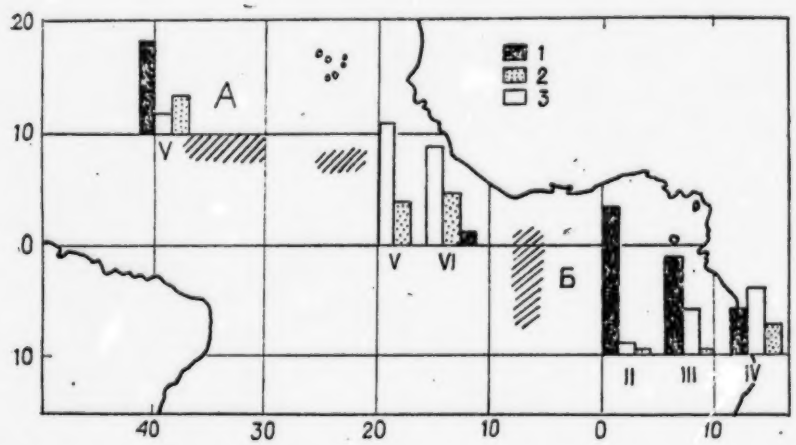

Fig. 1. Stages of maturity of bigeye tuna ovaries in the northern (A) and southern (B) regions:

1 - mature (IV, IV-V, VI-IV); 2 - maturing (III); 3 - immature (stages II, VI-II of maturity). Roman numerals designate the months

With differences in the structure of the migration cycles of bigeye and striped tuna of the Central-East Atlantic, the mechanism of intraspecies differentiation in these species is the same. Probably, the expansion of the

ranges of hypothetical single equatorial populations of each occurred with an increase in the extent of feeding migrations on both sides of the equator, in a region with an opposite-phased course of seasonal changes in physical factors and production processes. As a result, groupings with opposite-phased physiological cycles were formed, which can remain reproductively isolated even in the mixing zone in the equatorial waters of the northwestern part of the Gulf of Guinea. /33

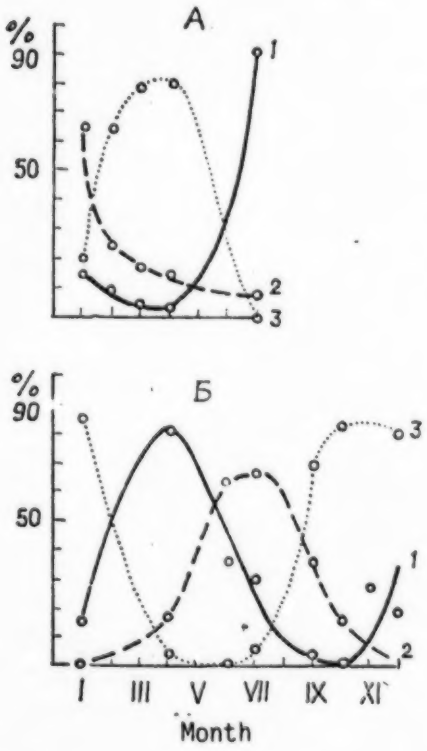

Fig. 2. Stages of maturity of the ovaries of striped tuna in the northern (A) and southern (B) regions:

1 - mature, 2 - maturing; 3 - immature

Beryx alfonsino. The expendable supply is formed according to the continuous type. Vitellogenesis is continuous-asynchronous, and spawning occurs in many batches (10-12 batches) with short intervals between the batches. The eggs are tiny, probably epipelagic. The fecundity is 0.8-2.3 million eggs [5]. The sexual cycles are reconstructed on the basis of fragmentary data from several regions of the species' range [13] of the Azores (I) and Uglovoi (II) Plateau in the Northern hemisphere and of the Vavilov Ridge (III) and Kitovoi Ridge (IV)

in the Southern hemisphere. The massive spawning of the Beryx of the Northern and Southern hemispheres occurs in opposite calendar periods - in June-August on the Uglovoi Plateau and in January-April on the Vavilov Range (Fig. 3). The reproductive cycles of these groupings are opposite-phased. Only large sexually mature individuals were noted in regions II and III, and immature individuals predominated in regions I and IV. In region IV, for which the data are most complete, it is impossible to reconstruct the sexual cycle on the basis of the seasonal distribution of the stages of maturity. Females with immature gonads (stages II and IV-II) predominate here from September to February. More than 60% of them occur in stage III of maturity in March and April, and in May their percentage drops against a background of an increase in the percentage of immature females. Maturing females predominate in July, and by September their percentage drops, but not as a result of their passage into the next phase of the cycle. The percentage of females with mature gonads is low year-round, and no spawning females are encountered. Evidently, as the gonads mature, Beryx migrates to the Kitovoi Ridge, to spawning regions which in every case occur beyond the banks under /34 investigation. Only sexually mature fish were caught on Vavilov Ridge. Spawning terminated in this region in April and May, and the gonads in most mature females were in stages VI-IV and V of maturity. The percentage of maturing (stage III) females varied from April to June/from 55 to 95%. Maturing females predominated in this region in October. On the basis of the presumed duration of individual spawning, we can assume that in the region of Vavilov Ridge it occurs roughly from December to April and May, and massive spawning - from January to March.

In the Northern hemisphere, a similar picture is observed, with the difference that spawning occurs from June to August (September). In the Azores region, immature fish predominate while the mature fish are mainly represented by maturing individuals. On the Uglovoi Plateau, from April to August, only sexually mature fish were caught: in April - maturing fish, in May to July --

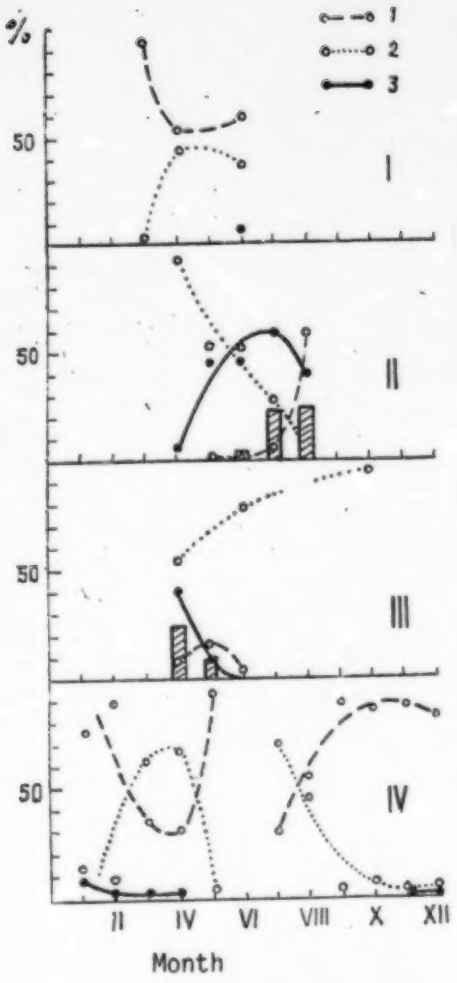

Fig. 3. Stages of maturity of Beryx eggs in the regions of: the Azores Plateau (I), the Uglovoi Plateau (II), the Vavilov Ridge (III), and the Kitovoi Ridge (IV):

1 - immature (II, VI-II); 2 - maturing (III), 3 - mature (IV, IV-V, V, VI-IV). The columns designate the percentage of spawning females (IV-V, V)

mainly mature and spawning fish, and in August - spawning and spent fish. The differentiation of Beryx, based on size, ratio of sexually immature fish to sexually mature fish and the stage of maturity of the gonads of sexually mature fish allows us to regard the Azores region and the Uglovoi Plateau as functionally different regions of the range of a single grouping with the main spawning /35 grounds on the Uglovoi Plateau. A similar supposition can also be made with respect to the Beryx of Vavilov Ridge and Kitovoi Ridge. Both pairs of plateaus - in the Northern and Southern hemispheres - are situated along the peripheries of large-scale circulations [12], such that the drift of pelagic eggs and fry can proceed in a direction from the established spawning regions, Vavilov Ridge and Uglovoi Plateau, to regions where the sexually immature contingent predominates but spawning is either not noted at all or rare, i.e. to Kitovoi Ridge and the Azores region. In any case, there is no doubt that each of the four regions examined is functionally a full-fledged range of local groupings but supplements one another individually (within these pairs).

Black scabbard. The expendable supply is formed according to the intermittent type, vitellogenesis is synchronous (frontal), spawning occurs once,

possibly once and over an extended period. The duration of vitellogenesis is approximately 2 years; immediately after spawning, the expendable supply of the next reproductive cycle is already formed by oocytes finishing the phase of vacuolization. Therefore, stage II of maturity is only characteristic of sexually immature females, and the differentiation of the sexually mature and sexually immature contingent presents no difficulties. The eggs are large, and the average fecundity is approximately 300 thousand eggs.

In the Azores region, only maturing and spent females were noted in July and September, and spawning females occur sporadically in July. On the Uglovoi Plateau, over a period of six months, from March to August, females with mature gonads predominated consistently, and massive spawning was noted. The percentage of fish in stage III of maturity was less than 10%. The six-month duration of spawning does not at all conform with the nature of spawning by this species. The dynamics of the stages of gonad maturity of the females of the Uglovoi Plateau region cannot be regarded as a reflection of the cyclical changes in the permanent contingent for the period of observation. There is no doubt that spent individuals are retained in the region of the black scabbard 's localized spawning grounds where the mature and spawning individuals concentrate. We can assume that the extension of spawning indicates that groupings from fairly large water areas with dissimilar conditions approach the spawning grounds. The Azores region and the Uglovoi Plateau probably represent functionally different regions of the range of a single grouping of black scabbard, and the analogy with the situation described for the Beryx of these two regions serves as an additional indirect argument in support of such an assumption.

Rock grenadier. Vitellogenesis is completed frontally, spawning occurs once for an extended period, or twice. The eggs are large, up to 3 mm, and the average fecundity is 27 thousand eggs [4]. Individuals with mature gonads are /36

noted from March to October, with the maximum from June to September. Increased percentages of sexually mature fish - among them, individuals with mature gonads - are observed over several years from the northern tip of the Reykjanes Ridge southwards to Gibbs Fault and the northern tip of the North-Atlantic Ridge (Fig. 4, 5). The entire region examined represents functional subdivisions of the range of a single grouping; the northern part is the region where sexually

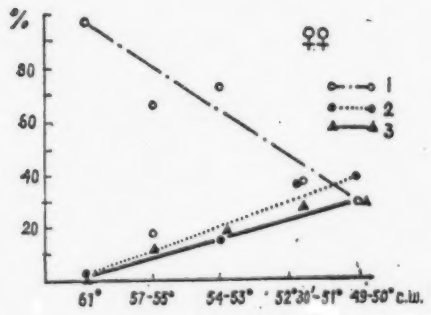

Fig. 4. The ratio of sexually immature (1), maturing (2) and mature (3) grenadier females on the North—Atlantic Ridge in June and July, 1981

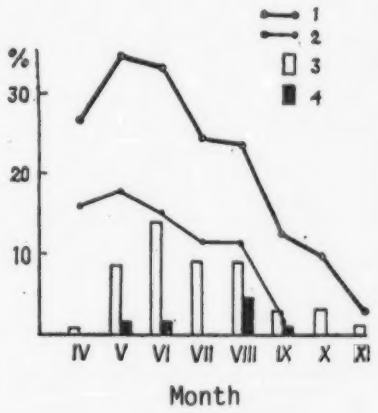

Fig. 5. Seasonal changes in the percentage of mature females (broken lines) and spawning females (histogram) in the northern (2, 4) and southern (1, 3) regions of the North-Atlantic Ridge in 1975-1978

mature and sexually immature individuals migrate to feed, and the southern part is the reproductive region [2]. Spawning occurs in the thalassobathyal region under the North-Atlantic current, and the bathypelagic eggs, pelagic larvae and fry drift for a long time in the system of the North-Atlantic and Irminger currents and are dispersed over the vast waters of the central and western parts of the North Atlantic. As the genadier grows, it migrates slowly in the reverse direction (ontogenetic migration) and reaches the reproductive region by the time it matures. The sexually mature contingent makes seasonal migrations on a smaller scale, mainly from the north to the south of Reykjanes Ridge (cyclic migration). Yu.Yu. Marti [18]

provided a similar picture, based on fragmentary data [18].

South-Atlantic grenadier. Vitellogenesis is lengthy, approximately two years, and frontal. Spawning occurs once over an extended period, or twice. After spawning, the eggs pass into stages VI-III and III of maturity. The /37 percentage of sexually mature individuals - among them, fish with mature gonads - increases in the Falkland-Patagonia region along the continental slope from north to south. In the south, sexually mature fish comprise over 90%, and only here is spawning noted. The functional differentiation of the range of this species is governed by the drift of the pelagic planktonic stages in the Falkland current system, and a similar picture is described for rock grenadier. The direction of passive (south to north) and active (north to south) migrations for both species is defined by the corresponding direction of the currents.

The fish briefly examined in the article were selected on the basis of a general characteristic: their biology and, in particular, the functional structure of the ranges and the intraspecies structure have been poorly studied or not studied at all. In such cases, a purposeful study of particular aspects of reproductive physiology and an analysis of reproductive cycles based on the data of bioanalysis can be effective and at the same time a fairly simple means of constructing working systems of the functional structure of ranges and the population structure.

CONCLUSIONS

1. There is sufficient theoretical basis for using the parameters of sexual cycles in the studies of the population functional structure of ranges of marine fish.

2. The subdivisibility of bigeye tuna and striped tuna of the Eastern-Tropical Atlantic is shown for reproductive isolates (populations) of the Northern and Southern hemispheres.

3. It is proposed that Beryx alfonsino is represented by two populations: those of the Uglovoi Plateau - Azores region, and of the Vavilov Ridge - Kitovoi Ridge; and black scabbard of the Uglovoi Plateau - Azores region is represented by one population.

4. The population unity and the distinct functional differentiation of the ranges of the rock grenadier of the North-Atlantic Ridge and of the South-Atlantic grenadier of the Falkland-Patagonia region were established.

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